A New Species of *Saccocirrus* (Archiannelida) from the West Coast of North America

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ABSTRACT: A new species of archiannelid, *Saccocirrus eroticus,* from shell gravel from Orcas Island, Washington, U.S.A., is described. The species is characterized by being 1 to 2.2 cm long when adult and comprising up to 125 body segments. It has unilateral gonads which begin in segment 13 and run to an achaetous region at the pygidial end; thus it has over 100 segments bearing reproductive organs. The achaetous region is composed of 4 to 11 segments. There are two tail lappets bearing 7 to 22 papillate ridges. The internal anatomy is described in detail and compared with other known species of *Saccocirrus.* Eggs released from females showed normal spiral cleavage and trocophores developed after 24 hours. The relationship of the saccocirrids to the protodrilid archiannelids and orbiniid polychaetes is discussed in relation to feeding and locomotory structure and function.

IN A BRIEF NOTE, Berkeley (1936) reported the occurrence of an unnamed species of the genus *Saccocirrus* in western Canada. On the basis of setae corresponding to *S. papillocerus* Bobtretzky and anal lobes resembling *S. major* Pierantoni, Marcus (1946) considered the Canadian species identical with a Brazilian species, *S. gabriellae* Marcus (1946). Alikunhi (1948) discovered another saccocirrid at Krusadai, India. The Indian species, *S. krusadensis* Alikunhi, and *S. gabriellae* are distinguished from all other known saccocirrids in having gonads on only one side of the body. Buzhinskaja (1967) and Scarlato et al. (1967) have reported *S. gabriellae* from coarse gravel in Possjet Bay, Sea of Japan. The development of this species was reported briefly by Marcus (1946). However, Sveshnikov (1967) described the larvae from Possjet Bay in more detail.

During a search for archiannelids in the San Juan archipelago, immense numbers of *Saccocirrus* were located in broken shells at Barnacle Rock, Orcas Island, Washington, U.S.A. On examination, this animal was found to have unilateral gonads but to differ markedly from the Indian and Brazilian species. Thus the description of a new species seemed justified. Little attention seems to have been given to the unique feature of unilateral gonads, described in detail by Alikunhi (1948) and Marcus (1946). With the exception of the latter two studies and the early work on *S. papillocercus* (Marion and Bobtretzky, 1875, and Goodrich, 1901) and on *S. papillocercus* and *S. major* (Pierantoni, 1907), no detailed anatomical studies have been undertaken on this genus. Therefore, the specimens of the new species were examined in detail.

Specimens of the *Saccocirrus* sp. found by Berkeley were obtained from the U.S. National Museum for comparison with the new species. As far as could be ascertained they are identical.

MATERIALS AND METHODS

A sample of shell gravel from just below low tide level at Orcas Island was collected in a plastic bucket and allowed to stand in sea water at 15°C. After 24 hours the surface of the sand was covered with 700 to 1,000 *Saccocirrus,* which were removed with a wide-mouth pipette and transferred to glass dishes (15 cm diameter) full of sea water. About 20 to 40 animals were placed in each dish with a small quantity of natural shell gravel. The dishes were kept at a temperature of 15 to 18°C, and the sea water,

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which was changed weekly, was kept at a salinity of 29 ‰. The animals remained healthy for more than 10 weeks under these conditions.

After being anaesthetized with magnesium chloride (73.2 g/liter), living animals were studied under a low power binocular microscope.

For anatomical study some adults were fixed in gluteraldehyde in Millonig's phosphate buffer, and embedded in epon. Sections 1μ in thickness were cut on an ultramicrotome and the sections stained with Richardson's stain (Richardson et al., 1960). These sections were photographed, and drawings were made from the photographs.

DESCRIPTION OF SPECIES

Saccocirrus eroticus n. sp.

EXTERNAL CHARACTERS: Mature worms measure 1.0 to 2.2 cm in length with a width of 300 μ to 330μ. The largest specimen measured (2.2 cm long) had 125 body segments and the smallest number of segments recorded was 4. The worms are mature at 70 segments (exceptionally at 50 segments). The color of the worms is a pale pink or white with a dark green intestine, which is visible through the body wall. The body wall itself is covered with irregularly shaped refringent inclusions. Figure 1 shows the dorsal (A) and ventral (B) views of the worm.

Two cup-shaped black eyes are situated just anterior to the tentacle insertions. The tentacles, which attain a maximum length of 920μ, have a number of large sensory setae over their whole surface. Between the tentacle insertions are a number of smaller sensory setae (see Fig. 1). As in the other known species of *Saccocirrus* two large tentacular ampullae act as reservoirs for fluid used in making the tentacles rigid or flaccid (Marcus, 1946).

Behind the eyes and at the posterior margin of the prostomium is a ciliated groove, the nuchal organ. The cerebral ganglia can be seen at the point where the tentacular canals anastomose. A pair of parapodia occurs on the head segment.

On the ventral surface of the head is a long slitlike mouth extending from a point level with the nuchal organ to three-quarters of the way down the head segment. This long mouth is strongly ciliated. At the posterior edge of the mouth is a raised funnel-shaped margin with a crenulated edge.

On both sides of the mouth there is a deep ciliated groove which joins to form a single ventral groove just behind the crenulated margin of the mouth (Fig. 1B and Fig. 4*c–d*). This ciliated groove, which continues to the middle of segment eight, is easily seen in transverse section (Fig. 4*k–l*). No previously known species of *Saccocirrus* has such a groove, and therefore this is of major taxonomic importance.

Parapodia, bearing chaetae, occur from the head segment to an achaetous region two to eleven segments from the pygidium (Fig. 2A). There is a small transition zone of reduced numbers of chaetae before the achaetous region, as is found in most other saccocirrids. The number of achaetous segments plotted against the total number of body segments showed an inverse relationship: the larger the number of body segments the smaller the number of achaetous segments. For example, worms of 100 body segments had 4 to 7 achaetous segments, whereas worms of 50 segments had 8 to 11 achaetous segments. The use of the number of achaetous segments as a taxonomic character, therefore, seems valueless. The achaetous region is merely a budding zone. The chaetae numbered from 6 to 8 in most body segments, smaller numbers being found on approaching the achaetous region (Fig. 2A). One long, finely forked hair chaeta, five or six unequally forked chaetae, and one spatulate chaeta per parapodium was the usual pattern (Fig. 2B).

On the two large caudal appendages were a number of papillate ridges. A plot of the number of ridges against the total number of body segments showed an increase in the number of ridges with the number of body segments. Worms with 50 body segments had an average of 7 ridges per appendage, those with 75 body segments 11 ridges per appendage, and with 100 body segments 15 ridges per appendage. However, many worms had damaged caudal appendages, which were being regenerated. These worms had smaller numbers of ridges than was the case in undamaged specimens. The maximum number of ridges counted was 22. The fact that the number of ridges varies with

the number of body segments suggests that the number of ridges must be used with care as a taxonomic character.

The richly ciliated anus lies between the bases of the caudal appendages.

MUSCLE SYSTEM: Inside the thin cuticle and glandular epidermis is a thin layer of circular muscle (Fig. 3A, B, C). This layer extends obliquely across the body cavity from a mid-lateral point to the nerve cords, a position similar to that in *S. papillocercus* (Marion and Bobtretzky, 1875), *S. major* Pierantoni, 1907), and *S. krusadensis* (Alikunhi, 1948). The longitudinal muscle consists dorsally of a thin layer inside the circular muscle and extends around to the oblique muscles. Ventrally, however, there are two large ventrolateral bands (Fig. 3A, B, C) with a thinner midventral muscle layer. This is the usual arrangement in those saccocirrids which have been examined in any detail.

LOCOMOTION: The youngest specimens of *S. eroticus* (up to 30 segments) move smoothly over the bottom using the cilia of their ventral surfaces. This type of locomotion is very similar to that of the protodrilid archiannelids.

However, with increasing size the following muscular locomotory pattern is used:

The tail lappets of *S. eroticus* are extremely glandular. With the lappets attached to the substrate, the head end of the worm is stretched out by beating of the cilia located on the ventral surface of the head, and by the contraction of the circular muscle of the body wall and relaxation of the longitudinal muscle. The head end is placed close to the ground during this movement and the tentacles and mouth sample the substrate. If the substrate is unattractive, the longitudinal muscles contract vigorously (see Fig. 3A, B, C for location of muscle blocks), and the worm, still attached by the lappets, samples in a new direction. The worms can stretch to three times their contracted length.

If the substrate is attractive the head attaches to the substrate, presumably by a form of suction from the mouth cavity. Initially the longitudinal muscles of the first third of the body contract, the tail lappets release their hold and the posterior portion of the worm is pulled forward. A wave of contraction passes posteriorly very quickly, and the whole tail end is pulled forward and a new point of attachment for the lappets is formed. When the longitudinal muscles are contracted, the chaetae are elongated and form points of attachment of momentary duration. The chaetae are especially noticeable when the worm is moving sinuously around sand grains.

Worms with damaged tail lappets, which are fairly common, use only the first third of the body in locomotion. The chaetae provide a point of attachment, and, by ciliary creeping (using the head cilia) and contraction of the circular muscle, the head is stretched out. The mouth forms the attachment point, the longitudinal muscles contract, and by releasing hold with the chaetal attachment the damaged posterior end is pulled forward. This whole sequence is carried out very rapidly.

If the worm is touched, it does not swim but curls up into a tight ball firmly attached to the bottom. Such a behavior pattern would serve to keep the animals from being washed out of the substrate by wave or current action.

ALIMENTARY CANAL: Transverse sections through the worm were made at the positions shown in Figure 1B (*a–b, c–d, . . . k–l*). These sections are shown diagrammatically in Figure 4. Section *a–b* is at the very anterior margin of the mouth. The mouth is here a shallow, ciliated groove. The ciliated nuchal organ shows on the dorsal surface. At section *c–d* the mouth is a deep, dorsoventral, ciliated groove with a distinct columnar cell lining. This lining is thickened ventrally with a lighter-staining area (Fig. 3A, B, C) which is probably glandular. Two well developed ciliated bands (*C.B.*) can be seen ventrally. The nerve cord (*N.C.*) in both sections *a–b* and *c–d* is distinct and ventrolateral in position. Figure 3A is a photomicrograph through the crenulated margin at the posterior edge of the mouth (*C.M.*). Two lateral diverticula are developing within the mouth cavity. Figure 4, *e–f* shows the closed mouth with the two lateral diverticula developing laterally. The lateral ciliated bands have merged into one groove, but the two bands are still distinct. Section *g–h* is the start of the pharynx, which is large and muscular and oc-

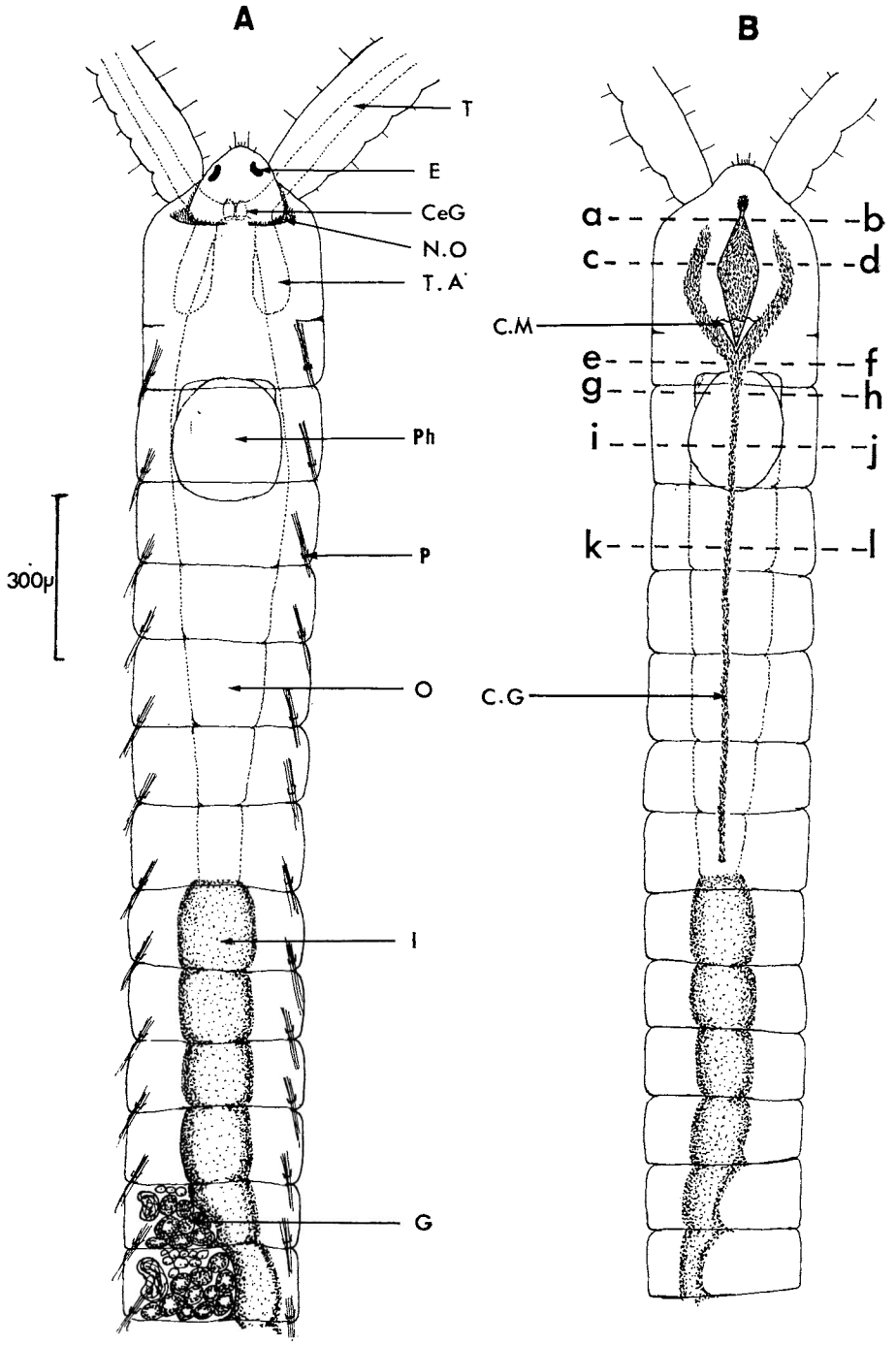
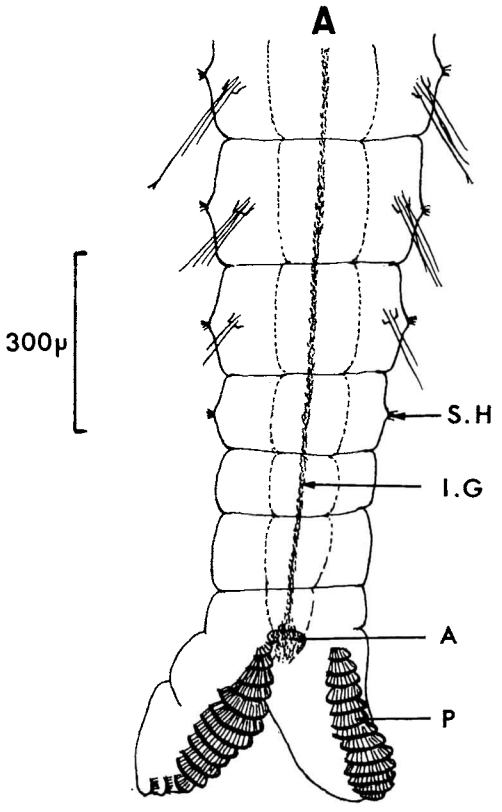


FIG. 1A (*left*). Dorsal view of anterior end of adult *Saccocirrus eroticus*. *CeG*, Cerebral ganglion; *E*, eyes; *G*, gonad; *I*, intestine; *N.O*, nuchal organ; *O*, oesophagus; *P*, parapodium; *Ph*, pharynx; *T*, tentacle; *T.A*, tentacular ampulla.

FIG. 1B (*right*). Ventral view of anterior end of *Saccocirrus eroticus* showing ciliation. *C.G*, Ciliated groove; *C.M*, crenulated margin of mouth. *a . . . b*, *c . . . d*, etc. indicate sections through the worm shown in Figure 3.



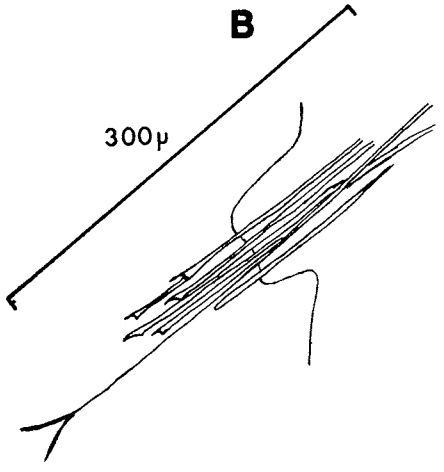


FIG. 2A (*top*). Posterior end of *Saccocirrus eroticus* showing achaetous budding zone and the tail lappets (ventral surface). *A*, Anus; *I.G*, intestinal groove; *P*, papillate ridges; *S.H*, sensory hairs.

FIG. 2B (*bottom*). Parapodium of *Saccocirrus eroticus* showing chaetae.

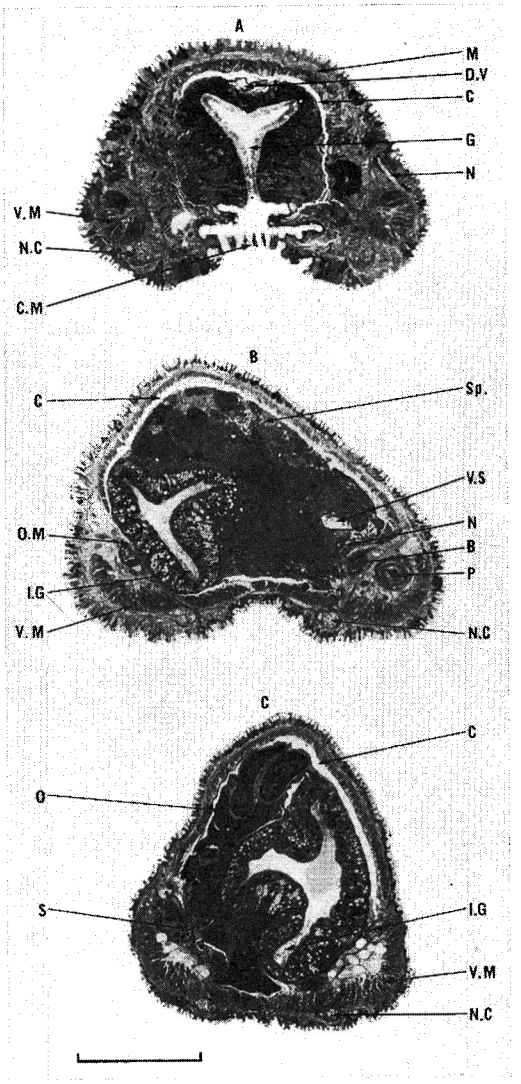


FIG. 3. Photomicrographs of transverse sections of adult *Saccocirrus eroticus*. (Scale = 100μ)

A: Through edge of mouth of adult worm. *C*, Coelom; *C.M*, crenulated margin of mouth; *D.V*, dorsal vessel; *G*, gut; *M*, circular muscle; *N*, nephridium; *N.C*, nerve cord; *V.M*, ventrolateral longitudinal muscle.

B: Through male worm. *B*, Chaetal bud; *C*, coelom; *I.G*, ciliated intestinal groove; *N*, nephridium; *N.C*, nerve cord; *O.M*, oblique muscle; *P*, penis; *Sp.*, spermatocytes; *V.M*, ventrolateral longitudinal muscle; *V.S*, vesicula seminalis.

C: Through female worm (structure basically as in male). *C*, Coelom; *I.G*, intestinal groove; *N.C*, nerve cord; *O*, oocytes; *S*, spermatheca; *V.M*, ventrolateral longitudinal muscle.

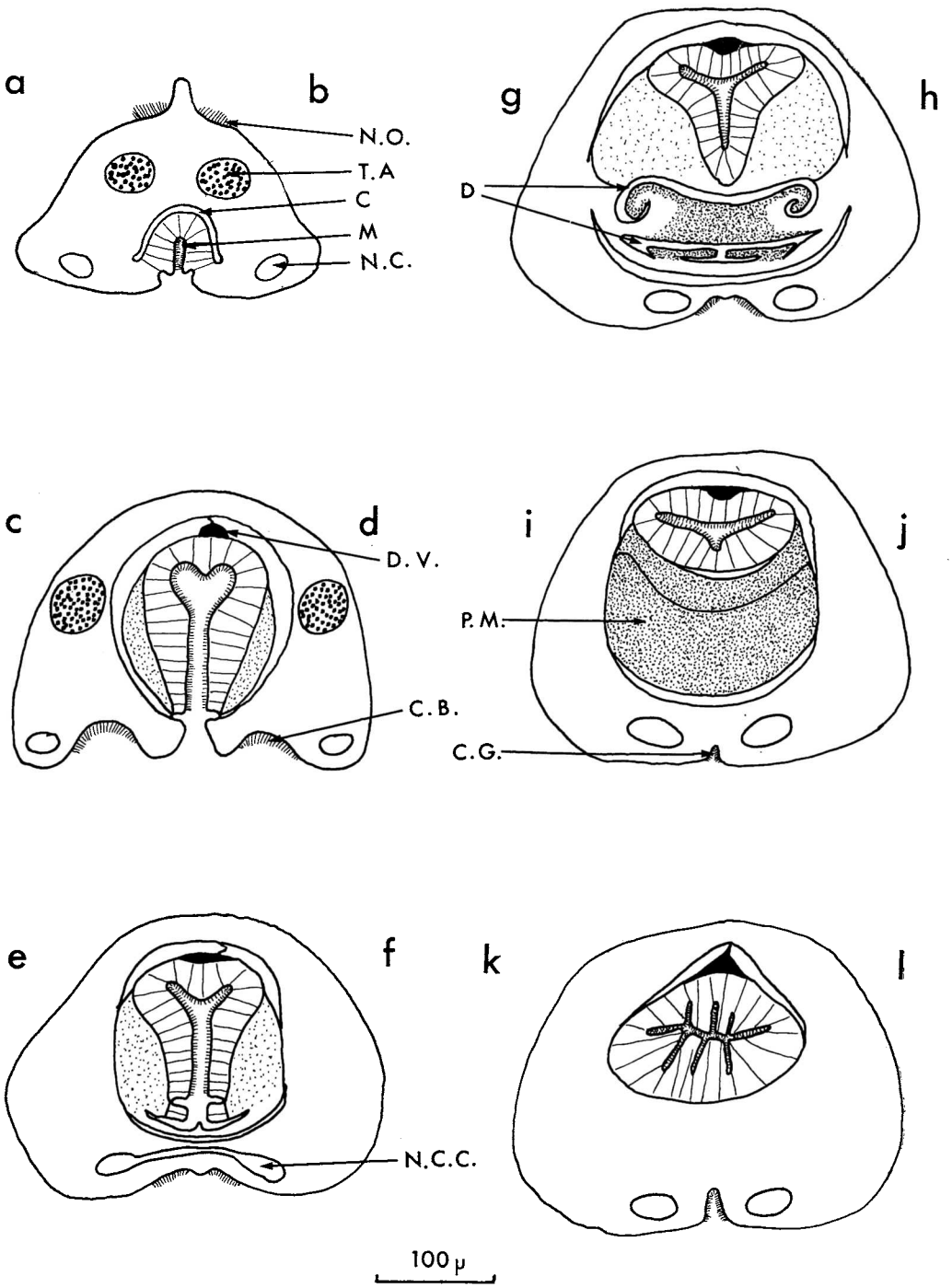


FIG. 4. Transverse sections through *Saccocirrus eroticus* taken at the positions shown in Figure 1B. *C,* Coelom; *C.B.,* ciliated bands; *C.G.,* ciliated groove; *D,* diverticula; *D.V.,* dorsal vessel; *M,* mouth; *N.C.,* nerve cord; *N.C.C.,* nerve cord commissure; *N.O.,* nuchal organ; *P.M.,* pharyngeal muscle; T.A, tentacular ampulla.

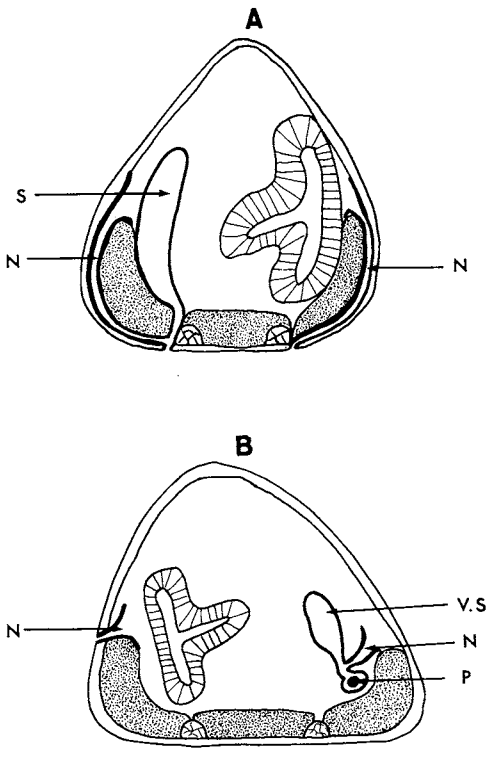


FIG. 5A and B. Diagrammatic representation of the arrangement of the nephridia and the gonads in *Saccocirrus eroticus*.

A: Female *S. eroticus* showing gut on right-hand side and gonads developed only on the left-hand side. *N*, Nephridia; *S*, spermatheca.

B: Male *S. eroticus* with gut on the left-hand side and gonads on the right-hand side. *N*, Nephridia; *P*, penis; *V.S*, vesicula seminalis.

cupies all of segment 3 and part of segments 2 and 4. Here the lateral diverticula (*D*) are much extended and a muscular layer occurs between each diverticulum. The lining of the diverticula is thick and cuticular as in *S. papillocercus* (Goodrich, 1901) and *S. krusadensis* (Alikunhi, 1948). In the mid-pharyngeal region (section *i–j*), the pharyngeal muscle is very well developed and only the more dorsal of the diverticula remains. This diverticulum does not extend for the length of the pharynx.

Posterior to the pharynx, beginning at segment 4, a light colored oesophagus (Fig. 1, *O*) extends to segment 8 or 9 (14 in *S. papillocercus* and *S. krusadensis*, 9–14 in *S. gabriellae*). The dark-walled intestine begins in segment 8 or 9 and runs to the anus. The whole of the gut is ciliated and the oesophageal region is glandular. The intestine is absorptive and covered with chloragogen cells giving it a dark-green color. A deep and ciliated ventral groove runs throughout the intestine and this groove can be seen through the body wall.

Use of the strong cilia of the ventral surface of the head sets up a strong water current. Bacteria, diatoms, and algae are drawn into this current from the shell gravel (around which the animal crawls), and into the mouth. The cuticular and highly muscular pharynx with its diverticula appears to have a mechanical crushing and sorting function. However, large diatom particles can be seen in the gut, almost filling the gut cavity, and so the exact role of the pharynx in the digestive process remains uncertain. The oesophageal region is glandular, and absorption occurs in the intestine. Food is moved through the gut by the cilia of the ventral groove since the gut does not have a well developed muscle layer.

NERVOUS SYSTEM: The normal pattern of saccocirrid nervous system is present, with a cerebral ganglion in the prostomium. Two cords run ventrally from the cerebral ganglion and are closely connected to the epidermis. These cords are ventrolateral in the head segment and become more median-ventral, posterior to the pharyngeal complex. No ganglia are found in the body segments.

As in *S. papillocercus* (Goodrich, 1901), a raised group of sensory hairs occurs dorsally to each parapodium.

VASCULAR SYSTEM: A distinct dorsal vessel lies in the coelomic cavity (Fig. 3A, B, C). The ventral vessel is less distinct but is present mid-ventrally in the coelomic cavity.

EXCRETORY AND REPRODUCTIVE SYSTEMS: The nephridia are extremely hard to see in the living worm and even in 1μ-thick transverse sections. Fig. 5A shows a duct running down between the body wall and the ventrolateral muscle, a position identical with that of the nephridia in the closely related *S. gabriellae*. The presence of a nephridium in the head segment, however, does not appear to have been recorded before in this genus.

The nephridia of the asexual region are very small and run between the body wall and oblique muscles. In the male they open laterally whereas in the female they open ventrally, as in *S. papillocercus* (Goodrich, 1901) and *S. gabriellae* (Marcus, 1946). The sexes are separate and the eggs can be seen clearly through the body wall in females.

The reproductive organs of *S. eroticus* start in segment 13 and continue to the achaetous zone at the posterior end. The gonads are unilateral, usually with male organs on the right-hand side looking anteriorly and female organs on the left-hand side (Fig. 3B, C). In the largest specimens there were up to 110 male or female reproductive organs, hence the name *S. eroticus*. In the reproductive segments the nephridia of the sterile side open to the exterior as in the asexual segments.

The nephridia of the reproductive side are closely connected to the reproductive organs and are similar to those of *S. gabriellae* and *S. krusadensis* (Fig. 5A, B).

In the female, a large curved spermatheca is connected by a long curled duct runnning along the segment and then passing through the ventrolateral muscle to a ventral opening. The nephridium is a fine narrow duct running from the septum along the segment outside the ventrolateral muscle. It fuses with the spermathecal duct ventrally in the middle of the segment (Fig. 5A), near the external opening. The oocytes arise on the posterior surface of the septum and develop in the coelomic cavity (Fig. 3C).

In the male there is a long uncuticularized penis, within a sheath, and connected by a short duct to the seminal vesicle. The penis typically lies parallel to the body wall and opens to the exterior midlaterally. The nephridium runs in the body wall from the septum to the base of the penis. Spermatozoa develop from the post septum and first appear as rosettes (Fig. 3B). The spermatozoa develop within the segment, and coiled sperms can be seen moving through the body wall.

Figure 5A and B show diagrammatically the relationship between the nephridia and the reproductive organs.

DEVELOPMENT: Light pressure on a cover slip covering a male specimen of *S. eroticus* causes the penes to protrude at the side of the worm (Fig. 6A). Although not observed under natural conditions, this is presumably the normal mode of copulation, impregnating females with sperm. It was found that 70 to 90 per cent of all the spermathecae in the two or three hundred females examined contained live sperm. Thus it would appear copulation had taken place.

Light pressure on female specimens under a cover slip causes release of large numbers of ripe eggs (ca. 90μ in diameter). As nearly as could be ascertained, these are released initially through the nephridia; when the pressure becomes too great, the body wall ruptures. Figure 6B shows eggs approximately 30 seconds after rupture of the body wall. Clearly, these eggs are from two segments, one of which had contained uncleaved eggs and the other, blastulae. Judging from squashes of a dozen or more females, the retention of cleaving eggs does seem atypical. Normally released eggs appear as the one shown in Figure 6C, and the fertilization membrane splits off within the first minute. The oocytes, therefore, must be fertilized within the female, and cleavage is arrested. This fact poses intriguing questions of fertilization mechanisms.

Anytime between 5 minutes and 1 hour after release from the female, the egg cleaves (Fig. 6D) giving two similar blastomeres; 45 minutes after the first cleavage the egg cleaves again (Fig. 6E). The next cleavage is unequal, giving micromeres and megameres. Figure 6F shows the egg 2 hours after release. After 5 hours a blastula is formed (Fig. 2G). With the suppression of cleavage within the female and rapid cleavage on release, accurate timing of divisions is difficult.

The ciliated gastrula stage (Fig. 7A) is reached after 12 hours. This gastrula has an outside wall of raised papillae 1 to 2μ long, and the cilia can be seen to arise from within this layer. After 24 to 36 hours, the early trocophore stage is reached (Fig. 7B). The trocophore has a distinct head cavity. By 48 hours the gut is well developed and an eversible pharyngeal region with long feeding cilia is produced (Fig. 7C). Unfortunately, I was unable to carry the developmental studies further due to lack of time.

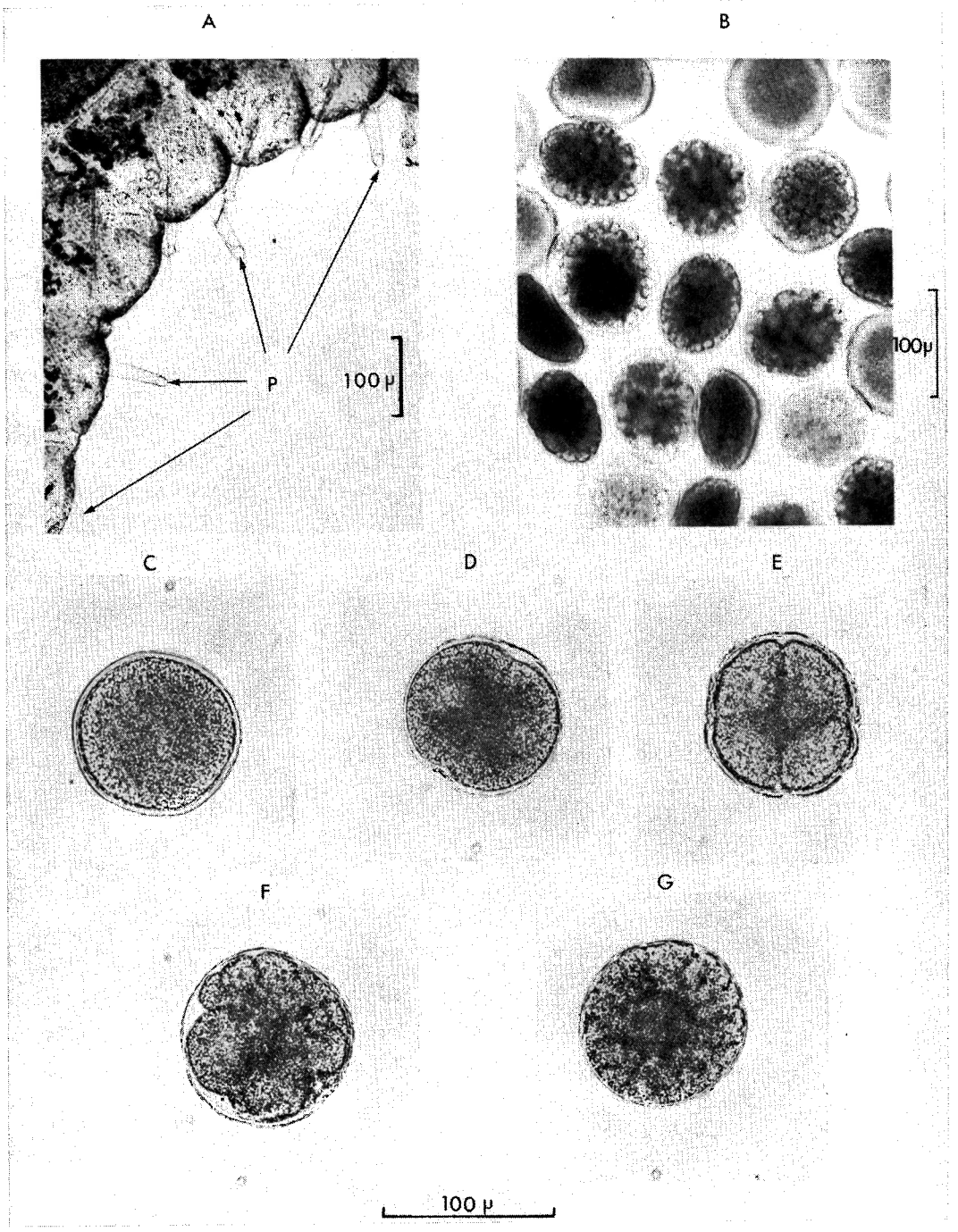


FIG. 6

A: Photomicrograph of living male *Saccocirrus eroticus* under light pressure, showing everted penes (*P*). B: Eggs released from female *S. eroticus* under light pressure. C: Egg just released from female. D: First cleavage 5 minutes to 1 hour after release from female. E: Second cleavage 45 minutes after first cleavage. F: Two hours after release. G: Five hours after release.

DIAGNOSIS: Pink-white worms 1 to 2.2 cm long and 300μ broad with up to 125 body segments; two distinct tail lappets at the posterior end with from 7 to 22 papillate ridges on each lappet; a ciliated ventral groove runs from behind the pharynx to segment 8; the gonads begin on segment 13 (12 or 14 occasionally) and are unilateral, only one side developing; the chaetae number up to 8 per parapodium; an achaetous region just anterior to the pygidium composed of 4 to 11 segments; cleavage of the egg is unequal and spiral, and development proceeds rapidly to give a trocophore larva.

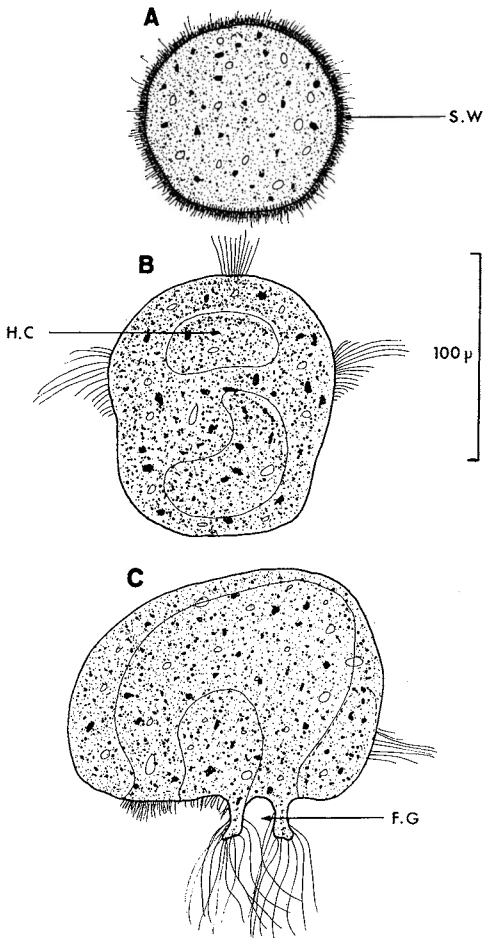


FIG. 7A, B, and C. Developmental stages of *Saccocirrus eroticus*.

A: Ciliated gastrula after 12 hours. *S.W*, Sculptured wall.

B: Early trocophore at 24–36 hours. *H.C*, Head cavity.

C: 48-hour trocophore showing everted fore gut with long cilia. *F.G*, Fore gut.

Differences from *S. gabriellae*: Smaller size, ciliated ventral groove from pharynx to segment 8, gonads beginning in segment 13 (29 to 35 in *S. gabriellae*), posterior margin of mouth more elaborate, shape of tail lappets different.

Differences from *S. krusadensis*: First segment behind head bears setae in *S. eroticus*; ciliated ventral groove present from pharynx to segment 8; gonads beginning in segment 13 (26 to 27 in *S. krusadensis*); more adhesive papillae in *S. eroticus* (up to 22, only 6 to 9 in *S. krusadensis*); intestine beginning on segment 8 or 9 (14 in *S. krusadensis*).

The holotype female is in the U. S. National Museum collection (Catalogue No. 36064), together with an allotype male (No. 36065) and 8 paratypes (No. 36066).

Saccocirrus sp. Berkeley (1936)

Re-examination of the preserved specimens in the U.S. National Museum collection showed that they are not *S. gabriellae,* as was assumed by Marcus (1946). The reproductive organs in Berkeley's specimens started at segments 10 to 12, which is more consistent with *S. eroticus.* Many of the important characters were hard to distinguish as *Saccocirrus* does not preserve well: the body becomes distended and the reproductive organs are hard to see. The gonads were apparently unilateral in the Berkeley specimens. The ciliated groove characteristic of *S. eroticus* is almost impossible to distinguish in preserved specimens.

The Berkeley *Saccocirrus* did have more achaetous segments than was usual in *S. eroticus,* but, as mentioned earlier, this may only be a factor of immaturity. Judging from their size and from the position of the reproductive segments, it seems likely that the Berkeley specimens are the same as *S. eroticus,* but re-examination of the living worms is necessary in order to clarify the point.

DISCUSSION

The two most unusual characters of this species are the unilateral gonads and the ciliated ventral groove. Most saccocirrids so far described possess normal bilateral gonads and

nephridia in the reproductive segments modified as gonoducts. *S. gabriellae* (Marcus, 1946), *S. krusadensis* (Alikunhi, 1948), and *S. eroticus* are unusual in that the gonads are unilateral and have modified nephridia on the gonad side of the reproductive segments and normal nephridia on the opposite side. Such an arrangement is remarkable, and little attention has been given to this fact. The nephridia are primitive in their close connection to the body wall musculature and in their presence in the head region. The functioning of the nephridia as gonoducts in the reproductive segments is known in *S. major* (Pierantoni, 1907) and *S. papillocercus* (Marion and Bobtretzky, 1875).

The selective advantage of unilateral gonads is difficult to postulate. Yet 70 to 90 per cent of the spermathecae in the females examined contained live sperm. Obviously, reproduction is easily accomplished. It seems likely, from observations of the live animals, that sperm is injected into the female segments and is stored in the spermathecae. Fertilization of oocytes has been reported to be precocious within the female of *S. papillocercus* (Baehr, 1920; Buchner, 1914; Gatenby, 1922; and Hempelmann, 1912), but examination of female *S. eroticus* under the electron microscope (Potswald, personal communication) showed no sign of fertilization within the female. Eggs released from squashed ripe females cleave immediately, and development is very rapid showing normal spiral cleavage. The ease of rearing the eggs to late trocophores (within 48 hours) in plain sea water does seem to make this species admirable material for fate map studies and studies on the mechanisms of fertilization.

Goodrich (1901) gave a lucid account of the relationships of *Saccocirrus* to the Polygordiidae. He states, "This group containing the genera *Polygordius, Protodrilus* and *Saccocirrus* we should regard not as ancestral to the Annelida, but as composed of specialized offshoots of the annelid stem (probably indeed, of the Polychaete stem)." Both Goodrich (1901) and Remane (1932) regard *Protodrilus* and *Saccocirrus* as closely related due to their possession of similar muscular pharyngeal bulbs, the presence of tentacular ampullae, and the widely separated unganglionated ventral nerve cords. To these similarities may be added the ciliated ventral groove of *S. eroticus* which surely indicates a close affinity to the ciliated ventral groove in the protodrilid family.

Recently, Jouin (1966) has formed a new genus *Protodriloides* to include *Pr. symbioticus* (Giard) and *Pr. chaetifer* (Remane), which were formerly considered members of the genus *Protodrilus*. Thus the Protodrilidae now include two genera, namely, *Protodrilus* and *Protodriloides*. The two species of *Protodriloides* show considerable changes in shape as compared with members of the genus *Protodrilus*.

In *Protodrilus* a thin layer of longitudinal muscle gives minimal locomotory power, and ciliary creeping is the main locomotory force. In *Protodriloides* the longitudinal muscles have changed from a uniform thin layer, and are arranged in blocks, closely resembling the position in *Saccocirrus*. The ciliation in *Protodriloides* is reduced (Jouin, 1966). *Pr. chaetifer,* as its name implies, has developed chaetae. Presumably, there has been a slow change within the Protodrilidae from a ciliary creeping form, as in most of the *Protodrilus* genus, to an increasing use of longitudinal muscles which become organized in blocks, with the development of adhesive organs (*Pr. symbioticus*) or chaetae (*Pr. chaetifer*) to serve as attachment points and assist in locomotion.

In support of this transition to better adaptation for locomotion within sand, the course of development has also changed. Whereas in all species of the genus *Protodrilus* a planktonic larva occurs, in *Protodriloides* development is direct and within a cocoon (Jouin, 1966).

Saccocirrus eroticus, in possessing a partly ciliated locomotion and a ciliated ventral groove, seems close to having the basic type of locomotory pattern occurring in the *Protodrilidae*. However, the longitudinal muscles are localized into distinct blocks and a thin circular muscle layer is present. Thus, gross shape changes can occur, as was the case in *Protodriloides*. With the lack of a ciliated ventral groove in the other members of the genus *Saccocirrus,* the contractions of circular and longitudinal muscles must provide the sole locomotory power. Thus, on the basis of locomotory characteristics, one might postulate that *Saccocirrus* and *Protodrilus* have a common ancestor and so may be closely related.

The extremely complex nature of the reproductive system in *Saccocirrus* as compared with that of *Protodrilus* is, however, more difficult to relate to this hypothesis, as both families live within similar substrates where selection pressures are presumably similar also.

Clark (1965) suggests that the earliest annelids developed when there was a change from the epibenthic creeping of the ciliated Protobilateria to a burrowing habit. Fundamental to the success of a burrowing animal was the possession of a well developed hydrostatic skeleton, longitudinal and circular muscles, and an eversible pharynx. Clark suggests that animals so equipped for burrowing subsequently changed to locomotion within and upon the substrate, thus giving the errant polychaetes.

It seems likely that the errant polychaetes could also have evolved from an interstitial ciliary creeping form. Ciliary creeping is well developed in interstitial forms (Swedmark, 1964). Even *Protodrilus rubropharyngeus* Jägersten, which is 1.5 cm long, moves by the cilia of its ventral surface, and lives in the interstitial spaces of sand. Just as a circular cross section is pre-adapted for burrowing (Clark, 1965, p. 94) so is it also adapted for movement within the sand interstices. If, in its feeding, an interstitial species scrapes particles from the sand grain surfaces, one would expect the mouth to be ventral and to be closely applied to the sand grain surfaces. Thus the presence of a ventral mouth in the archiannelids does not necessarily imply that the animals are epibenthic, as was suggested by Dales (1962), but merely indicates that they are epistrate feeders.

The similarity between their muscular pharyngeal complex has been suggested as linking archiannelids to larval orbiniids and adult cirratulid polychaetes (Dales, 1962). Anderson (1959), studying the development of the orbiniid polychaete *Scoloplos armiger* O. F. Müller, shows sections of the 11-day larva which clearly show the similarities of the pharyngeal mass to that of *Saccocirrus eroticus* (Fig. 8). Both feed by using the buccal complex for sampling sand grains. In the transverse section of *Scoloplos armiger* (Fig. 8A), the arrangement of the muscle system is remarkably similar to that of *Saccocirrus eroticus* (Fig. 3). There is a thin layer of circular muscle (*C.M.*) with a ventrolateral thickening of the longitudinal muscles, just as in *S. eroticus*.

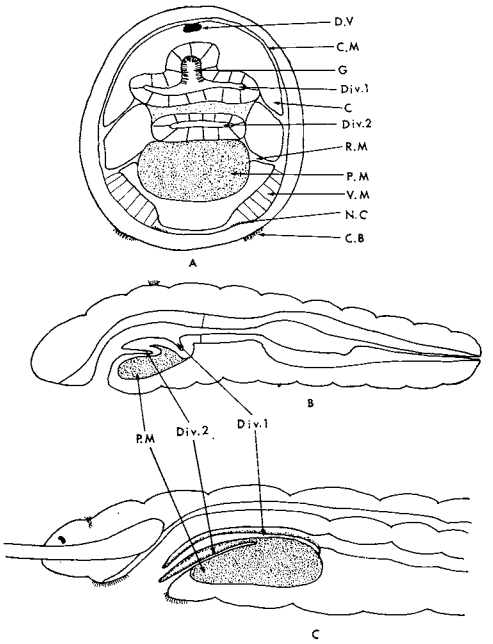


FIG. 8A, B, and C. Comparison of the 11-day larva of *Scoloplos armiger* (from Andersson, 1959) with *Saccocirrus eroticus*.

A: Transverse section, 11-day larva of *Sc. armiger* (compare with *S. eroticus*, Figure 4, *i–j*, and Figure 3A). *C*, Coelom; *C.B*, ciliated band; *C.M*, circular muscle; *Div. 1*, diverticulum 1; *Div. 2*, diverticulum 2; *D.V*, dorsal vessel; *G*, gut; *N.C*, nerve cord; *P.M*, pharyngeal muscle; *R.M*, retractor muscle of pharynx; *V.M*, ventrolateral muscle.

B: Longitudinal section, 11-day larva of *Sc. armiger* showing pharynx and diverticula. *Div. 1*, diverticulum 1; *Div. 2*, diverticulum 2; *P.M*, pharyngeal muscle.

C: Longitudinal section, head of adult *S. eroticus* showing similarity with larval *Sc. armiger*.

Up to the 9th and 10th day *Scoloplos armiger* moves by means of cilia on the ventral surface. By the 11th day the cilia are lost and the larvae show spasmodic irregular peristalsis, and an irregular forward progression results. Thus, coordinated musclar locomotion first occurs in *Sc. armiger* in the 11-day embryo.

The developmental change from ciliary creeping to a muscular locomotion closely resembles that of the change from ciliary creeping in *Saccocirrus eroticus* to a muscular locomotion in other saccocirrids.

The septa of the protodrilids are thin, non-

muscular, and incomplete (Jouin, 1966). *S. eroticus, S. gabriellae,* and *S. papillocercus* have non-muscular septa whereas in the largest saccocirrid, *S. major,* the septa are muscular. Increasing use of a muscular locomotory system produces an increase in the development of the septa, associated with higher coelomic pressures.

It may be argued that this series shows a progressive simplification from a muscular locomotory system to ciliated locomotion within the interstitial spaces. The primitive characters of the saccocirrids—serially repeated gonads and nephridia; widely separated, unganglionated, double ventral nerve cord; a thin layer of circular muscle; non-muscular septa; ciliary creeping in *S. eroticus*—suggest to me a closer affinity to a hypothetical polychaete ancestor than to a secondarily reduced polychaete.

Whereas ciliated species are confined to locomotion within the sand interstices (or upon the sand surface), the presence of a well developed muscle system enables the animals to push the grains apart. Thus the animals with well developed circular and longitudinal muscles become independent of the size-restricting properties of ciliary locomotion within the interstices. Saccocirrids are larger than the protodrilids, and orbiniids in turn are larger than saccocirrids, showing a trend toward increasing use of muscle systems in locomotion. Once the muscular locomotory system was established, the great range of errant polychaete radiation could evolve.

The similarity in the structure (and derivation from stomodaeal ectoderm) of the pharyngeal complex in saccocirrids and in *Scoloplos armiger* (Fig. 8B and C) suggests that they are probably homologous (Dales, 1962, pp. 421–422). Dales believes such an apparatus arose in the archiannelids in relation to deposit feeding and this type of structure is ancestral to other polychaete feeding structures. If this is so, saccocirrids and *Sc. armiger* are undoubtedly closely related and primitive.

Further studies of archiannelid-polychaete relationships, such as that of Hermans (1966) showing affinities between *Polygordius* and the opheliid *Armandia brevis* Moore, might help to solve some of the problems of polychaete ancestry.

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